FISHES OF THE GENUS *SAROTHERODON* (PISCES, CICHLIDAE) OF SPRINGS ALONG THE NORTHERN UASO NGIRO, KENYA

K.L.I. Campbell
Biology Dept., University of Exeter, Devon, England

ABSTRACT

Cichlid fish of the genus *Sarotherodon* inhabit the Northern Uaso Ngiro and springs along its southern bank. The springs are warm (30—31°C) and their fish populations are now isolated from each other and from the river. The Uaso Ngiro is within the general area of distribution of *S. spilurus* (Günther) and although the related fish from the river were given a specific name (*Tilapia nyirica* Lönnberg), this has since been synonymised with *S. spilurus*. The types of *Tilapia percivali* (Boulenger 1912) also came from one of the springs and the taxonomic status of this population is still uncertain. Structure and ecology of fish from six springs are described. A purely microphagous diet in one population was correlated with a significantly longer intestine. Another population efficiently consumed snails, an unusual diet for *Sarotherodon*. The fish in all the springs do not exceed 120 mm total length and the phenomenon of precocious breeding was observed. A section is devoted to the microbranchiospines, their ontogenetic development and occurrence. The origin of the population is discussed in relation to the geological history of the area.

INTRODUCTION

Cichlid fishes of the Uaso Ngiro, a river in northern Kenya, belong to the genus *Sarotherodon*, formerly included as a subgenus of *Tilapia*, but recently raised to generic rank, (Trewavas *et al* 1972; Trewavas 1973). This river contains a single species named *Tilapia nyirica* by Lönnberg (1911), synonymised with *Tilapia nilotica* by Boulenger (1915) and later referred to as *Tilapia mossambica* by Whitehead (1962), but as *Tilapia spilurus* by Trewavas (1966). The last two authors consider it identical with the species of *Sarotherodon* that characterises the eastward flowing rivers of Kenya (Athi, Tana and shorter rivers).

Springs flow into the Uaso Ngiro in several places along a 65 km section of river near Archer's Post, (fig. 1.). Springs at Chanler's Falls contain fish described as *Sarotherodon percivali* (Boulenger 1912), whilst upstream at Buffalo Springs the fish were described as dwarf *S. mossambica* (Whitehead 1962). *Sarotherodon* from six springs along the Uaso Ngiro were studied in their natural habitats and in aquaria, and as preserved specimens.

THE STUDY AREA

The springs that flow into the Uaso Ngiro are fed by ground water arising in the Nyambeni Hills to the south. The water in all springs is clear and strongly contrasts with the river, (the name Uaso Ngiro means 'muddy river' in the local Samburu language).

To the south of the river large areas are covered by calcareous lake deposits, (Williams 1966 and Jennings 1967). These were laid down in natural dams formed by a combination of the existing basement systems hills and lava flows from the Nyambeni Hills. Intercalations of lava and sediment suggest a succession of such dams. In the fossiliferous sediments three species of Gastropod are found: *Melania tuberculata*, *Lemicolaria rectistringata* and a *Planorbis* sp. By far the most common is *M. tuberculata* which was found living in the present day springs.

It is not certain when the springs were first formed, but it is likely that they have been in existence since the lakes were first formed. Fish living in these lakes were faced with a slowly decreasing volume of water until they were confined to the present springs.

Only in two springs were other species of fish observed. *Labeo cylindricus* was seen in springs D and F, both of which contained a larger volume of water than the other springs. Isolation of each spring was
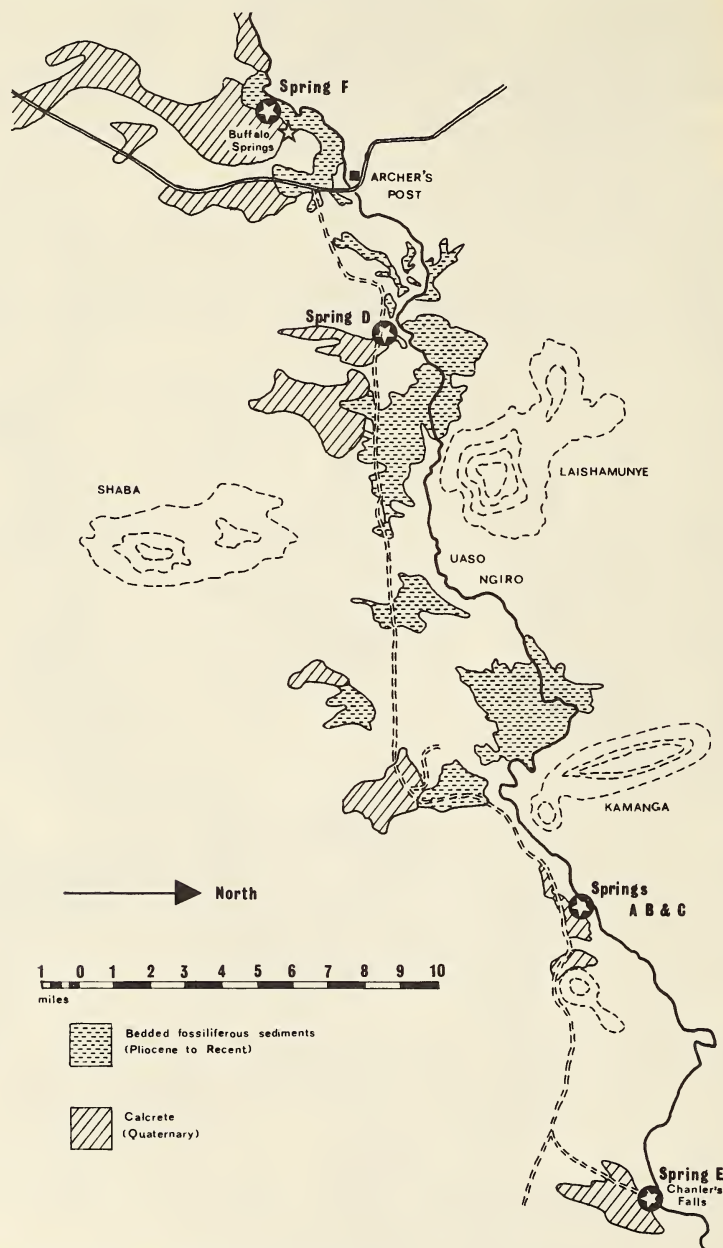
Fig 1 Map showing areas of sedimentation in the study area

provided by a series of waterfalls to the river itself, usually a drop of more than two metres. Flood waters may cover parts of some springs during periods of exceptionally high rainfall, and thus allow for a limited genetic interchange with the river. Flood waters can also be used to explain the presence of three *Barbus* which were observed in Spring A in 1972, but which were not present at the time of the study. However, debris deposited by the more recent floods indicated that this would only occur after exceptionally heavy rain in the headwaters of the river and probably never occurs in several springs.

At Buffalo Springs no adult fish were found, only two groups of about 40 small fry. This absence of larger fish can be attributed to the presence of fish predators. These included terrapins and three species of birds: *Phalacrocorax africanus*, *Ibis ibis* and *Ephippiorhynchus senegalensis*. Although no doubt a few

larger fish were present but not seen, the total number of breeding fish was small. The almost total removal of fish in this manner must have occurred many times in the past.

All the springs were formed in fossiliferous limestone rock. Springs A and B, although close together, were considered separately since movement from one to the other was considered impossible. About 40 m from the river, Spring A contained three pools between 15 and 115 cm deep and from 8 to 96 m² in area. These were joined by small streams up to 15 cm deep. Larger areas of what was once open water had been overgrown by sedges so constricting the fish to the present pools. Spring B consisted of a single stream not more than 3–5 cm deep and 40 cm wide heavily overgrown in parts by sedges. Spring C was approximately 400 m from the first two, 60 m from the river and consisted of a single pool up to 30 cm deep and 3 m² in area, with a small stream flowing to the river. Spring D was approximately 2 km from the river and consisted of a stream with pools up to 4 m wide flowing into a swampy area before reaching the river. Spring E was located immediately above Chanler's Falls and consisted of two pools, one of 120 m² having been dammed up in 1943, the other of 4 m² separated by a small patch of damp ground and having a separate exit to the river, 50 m distant. Spring F was situated about 10 km north of Buffalo Springs and consisted of a spring fed stream flowing for about 1 km before reaching the river.

The water temperature in all springs was found to be constant at 30–31°C, whilst the air temperature varied between 20 and 43°C.

Attempts to catch fish in the river met with no success.

MERISTIC CHARACTERS

Anal Spines and Soft Rays.

Anal spine counts were carried out on live fish from four springs, and on preserved specimens. Soft rays were counted only on preserved specimens, the last two rays being considered separately unless the last was very small. (This also holds for the soft rays of the dorsal fin).

Examination of the interhaemal pterygiophores showed that the first two spines were carried on the first pterygiophore, the rest of the spines being carried separately.

The modal number for each spring was three. The presence of a fourth spine was in some cases associated with a number of soft rays reduced below the mode. The modal number of soft rays is nine, except in Spring E (*S. percivali*) where it was 10, (see Table 1).

TABLE 1

Numbers of anal spines and soft rays

Spring	Anal Spine count			% 4-spined	No. of anal rays			
	2	3	4		8	9	10	11
A	1	106			4	17		
B		11			1	10		
C		28	7	20	1	7		
D		54				9	3	
E		56				1	5	6
F		7	2	22	1	5	2	1

The Buffalo Springs population of *Sarotherodon* examined by Whitehead (1962) had, in a count of 90 fish, 36% of four-spined individuals. The four-spined condition found in Spring C may indicate the degree of isolation between the different springs, especially as in this case only 400 m separate this population from the three-spined population of Spring A. One of the 9 syntypes of *S.percivali* (Spring E) has four anal spines (Trewavas pers.comm.) a condition not found in the present population in a sample of 56 fish.

Dorsal Spines and Soft Rays.

These were examined on preserved specimens and the results are tabulated below. *S. percivali* from Spring E, appears to be clearly differentiated by the presence of fourteen spines in 42% of the specimens, this condition not occurring in fish from any other spring. The fourteen-spined condition is derived from the fifteen by loss of the first spine. The pterygiophore of this first dorsal spine is reduced and forms a small projection visible in front of the second dorsal spine, either to the left or right of the midline according to the position of the second dorsal spine. This position bears no relation to the number of fin elements.

TABLE 2

Numbers of dorsal spines and soft rays

Spring	Dorsal spine count				No. of Dorsal Rays			Mean Total
	14	15	16	17	10	11	12	
A		6	5		3	7	1	26.18
B		1	10		5	6		26.45
C		4	2	1	1	2	4	27
D		1	11		2	9	1	26.75
E	5	7				6	6	26.83
F		1	8		6	3		26.22

Gill Rakers.

The total number of gill rakers on both inner and outer series were counted on each gill arch. Taking the first gill arch alone no significant difference was found, but, considering the total number of rakers, fish from Spring D have more and from Spring E less than the other four springs examined.

TABLE 3

Mean number of gill rakers on anterior and posterior faces of both branchial and epibranchial

Spring	No.	Gill arch 1		Gill arch 2		Gill arch 3		Gill arch 4		Mean Total
		ant.	post.	ant.	post.	ant.	post.	ant.	post.	
A	12	17.4	20.8	22.2	21.7	23.2	21.3	21.2	28.2	176.2
B	11	18	20.2	22.6	20.2	22.6	20.4	22	27.2	173.2
C	7	18.4	21.6	20.8	21.4	20.8	21.2	22.2	28.4	174.8
D	12	17.5	23.1	22.6	21.7	23.3	23.3	24.6	30	186.4
E	12	18.3	20.3	20.2	19.5	20.9	19.9	21.9	25.7	166.6
F	9	19.2	20.5	20.9	20.5	23	23	24.7	29.7	171.7

Scales.

The total number of pored scales in both lateral lines were counted. The transverse row of scales was counted starting from the base of the first dorsal spine, or in fish from Spring E, the position of the first pterygiophore, when the first dorsal spine was absent. The scales in the longitudinal row including the lower lateral line were also counted. *S. percivali*, from Spring E, have a higher mean scale count on the transverse row, and a smaller count on the longitudinal row.

TABLE 4

Number of scales in the lateral lines, length and depth

Spring	No.	Lateral lines	Transverse row	Longitudinal row
A	12	33 — 36	9 (10.1) 11	27 (28.9) 31
B	11	31 — 37	9 (9.8) 11	26 (27.9) 30
C	7	32 — 35	9 (9.3) 10	27 (28.4) 29
D	12	33 — 36	9 (10) 11	26 (27.2) 28
E	12	30 — 35	11 (11.7) 12	25 (26.4) 27
F	9	33 — 38	10 (10.5) 11	29 (29.8) 31

Caudal Peduncle.

The ratio of the length and depth of the caudal peduncle was calculated for each specimen examined. Results indicated that *S. percivali* (Spring E) has a deeper caudal peduncle than the other populations examined. Although there is an overlap, the maximum ratio recorded from *S. percivali* is below the means recorded from all other populations.

Premaxillae.

Distinct differences in the shapes of the premaxillae were seen. A prominent difference was the presence of a thickened portion of the premaxilla at the apex of the jaw in some populations. This was more
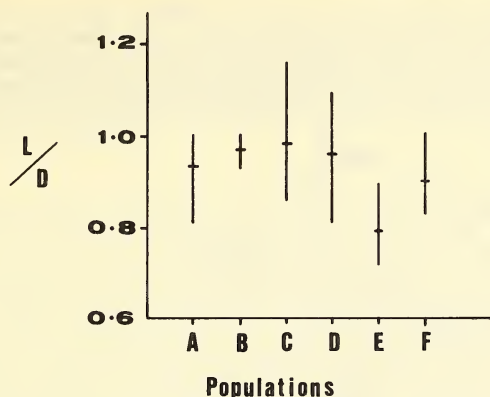
Fig 2 Means and range of the ratio length over depth of the Caudal Peduncle

fully developed in fish from Spring A, and seen also in Springs B and C. It is noticeably absent in fish from Spring E collected during the present study. However, the syntypes of *S. percivali* (collected 1912) show an enlarged premaxilla as seen in fish collected from Spring A (see fig. 3).

The angle formed by the premaxilla and the premaxillary pedicel was also found to vary. This accounts for the more convex profile seen in *S. percivali*.
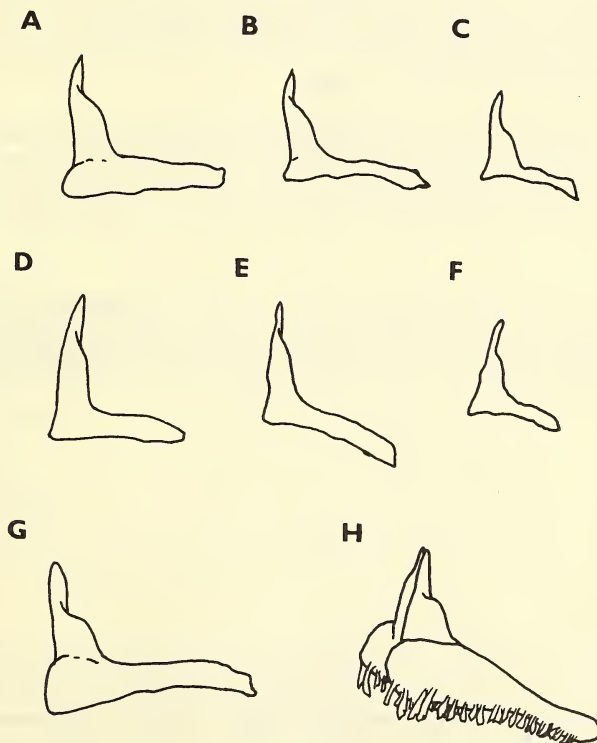
Fig 3 Premaxillae from the six populations studied:
A-F from Springs A to F (T.L. 65-75 mm)
G large specimen from Spring A (T.L. 101 mm)
H from syntype of *S. percivali* (S.L. 54 mm) from Chanler's Falls, collected 1912 (Spring E)
—after a diagram supplied by E. Trewavas, British Museum (Nat. Hist.)

No differences were seen in the profiles of the lower jaw. Larger male fish, of more than 100 mm examined in Spring A, show enlarged jaw profiles (fig. 4). This is also found to a lesser extent in large females, but its function is obscure. In males this no doubt aids in the excavation of breeding pits, though whether this is its main function is debatable. In fish observed both in the wild and in aquaria, this was accomplished solely by using the mouth. This method is also employed by *S. alcalica grahami*
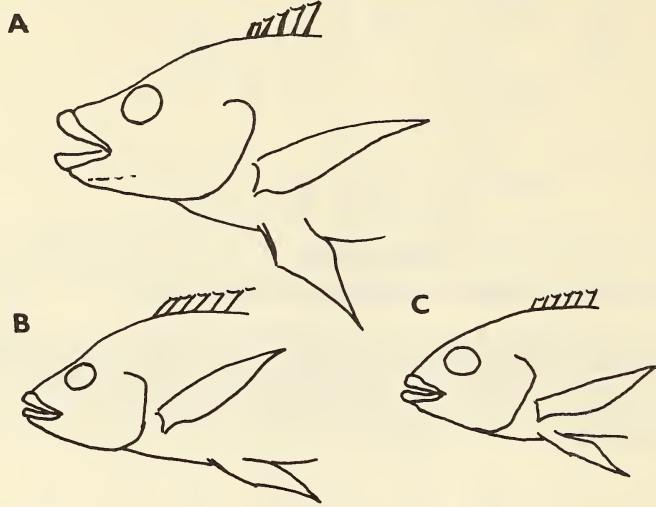

Fig 4 Head profiles showing:
　　A Enlargement of jaws in a large male from Spring A (T.L. 124 mm)
　　B Male from Spring D (T.L. 52 mm)
　　C Male from Spring C, *S. percivali* (T.L. 55 mm)

(*T. grahami*) Coe (1966). *S. niloticus,* which does not show this feature is known also to use tail movements in pit construction (Fryer & Iles, 1972). It is possible that this jaw enlargement, found in all *Sarotherodon* species from the eastward flowing rivers of Africa, enables breeding pits to be excavated in rivers. The sediment formed in lakes will be much lighter and tail movement would often be sufficient for the formation of a pit.

Gut Length.

Gut length was measured in fish within the size range 60—100 mm total length. The difference found in those fish from Spring D was statistically significant, (P : 0.001). In only a single fish out of 50 examined was a pyloric caecum found. In several fish a muscular thickening of the intestinal wall was seen a short distance beyond the stomach. This feature may assist where whole molluscs are eaten.
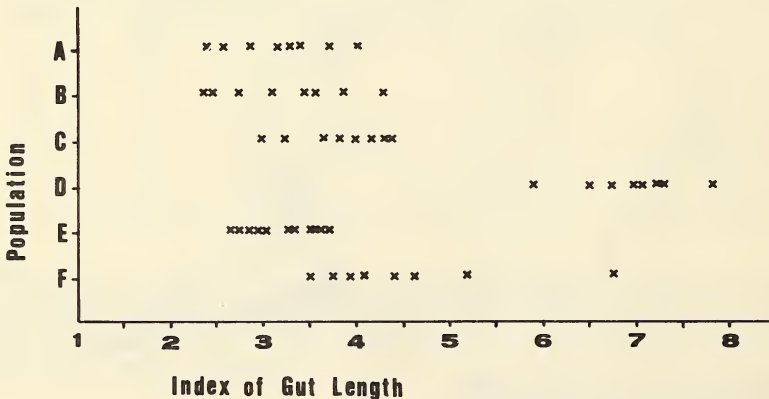

Fig 5 Index of gut length $\left(\frac{\text{gut length}}{\text{total length}}\right)$

Dentition.

S. percivali from Spring E was found to have a high proportion of tricuspid teeth in the outer series of the upper jaw. This was particularly evident at the posterior margins. In the remaining populations bicuspid teeth were found at the apex of the jaw and simple conical teeth at the posterior margins.

The pharyngeal dentition was found to be similar in all populations, with *S. percivali* having a slightly smaller tooth area than the others.

DIET

The contents of the stomachs and intestines of between five and ten fish from each spring were examined and feeding behaviour was observed at each spring except F.

Fish from Springs A, B, and C were found to have very similar diets, the only difference being the presence of *M. tuberculata* in the diet of Spring A fish. These were found to the exclusion of other food items in several specimens. Ostracods found in the intestines all had broken shells, whilst the majority of the *M. tuberculata* shells were complete or nearly so, containing snails. Observations in the field indicated a regular diet of *M. tuberculata* in Spring A. Some of these were removed from their shells before being swallowed. This was accomplished by obtaining a purchase on part of the snail and by movements of the jaws slowly extricating it from the shell. Several individuals were observed to eat a succession of snails in this fashion. Fish from the same spring on being transferred to an aquarium, also consumed in like fashion snails of a different species found locally in Nairobi. Other methods of eating observed in this spring were scraping off the aufwuchs from the rocks and feeding off detritus from the bottom, digging into it and expelling particles through the gills.

The fish in Spring D were shown to be primarily detritus feeders. This correlates with the longer alimentary canal found in these fish. The protozoans found in specimens from Spring F measured 8 by 12 μm and since no fine sediment was found it is apparent that they were not derived from the detritus.

Where alga was found in the intestines it was frequently contained within balls of mucus. Whitehead (1959) mentions similar balls of mucus in *Tilapia nigra* (*S. spilurus*). That the digestion of algae was incomplete was shown by obtaining photosynthesis from rectal samples taken from live fish. The small size of much of the food material indicates an active filtration system capable of retaining small particles.

TABLE 5

Stomach contents

Items of diet	Fish from Springs					
	A	B	C	D	E	F
Plant roots	*	*	*	*	*	
Four celled green algae	*	*	*		*	*
Unicellular green algae	*	*	*		*	*
Filamentous algae	*	*	*		**	
Diatoms	**	**	**	****		
M. tuberculata	***					
Ostracods	*	*	*			
Protozoans				*		****
Insect remains	*		*		*	
Fine sediment	*			***		

Microbranchiospines.

The second, third and fourth gill arches have, on their outer faces and some inner faces, a series of structures termed microbranchiospines or microrakers (see fig. 6). As no evidence of any 'raking' function was found, the term microbranchiospines is to be preferred. These structures are known to occur in most *Tilapia* and *Sarotherodon* species, and whilst they are known to occur in many *Haplochromis* species, the full extent of their distribution within the Cichlidae is unknown. Similar structures are seen in *Citharinus gibbosus* (Gosse 1956).

Each microbranchiospine consists of an outgrowth of the epidermis in the region immediately posterior to the gill-rakers. Within the microbranchiospine is an open horseshoe–shaped bony base which supports a row of denticles. These latter are formed of bone and dentine (Gosse 1956) and are divided at their bases to form forked roots which are attached to the bony plate.
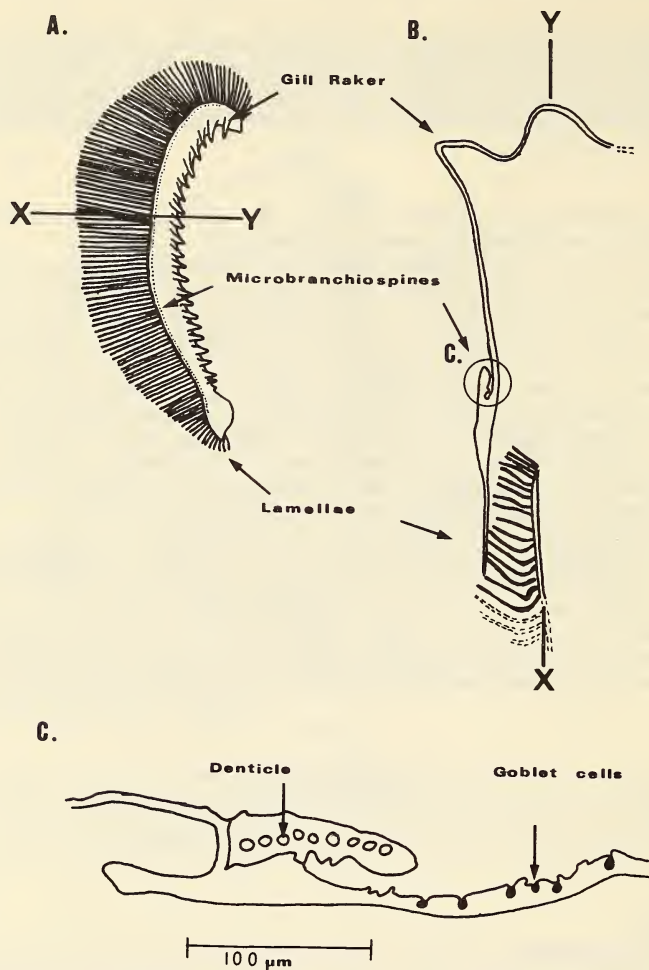
Fig 6 A   Anterior face of second gill arch, showing positions of microbranchiospines
      B-C   Enlargements of a transverse section
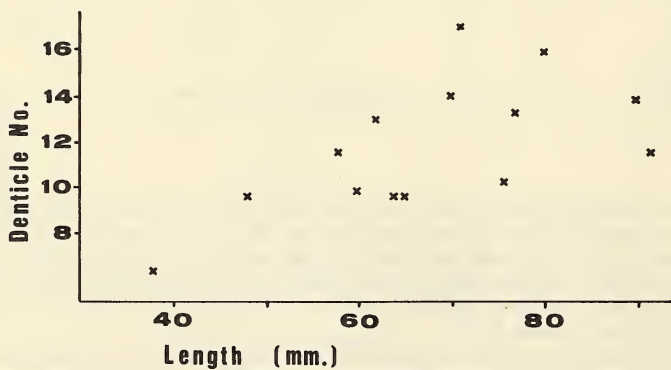   X-Y   Through the gill arch showing a single microbranchiospine

Fig 7 Correlation between mean denticle number per microbranchiospine and total length of *Sarotherodon*
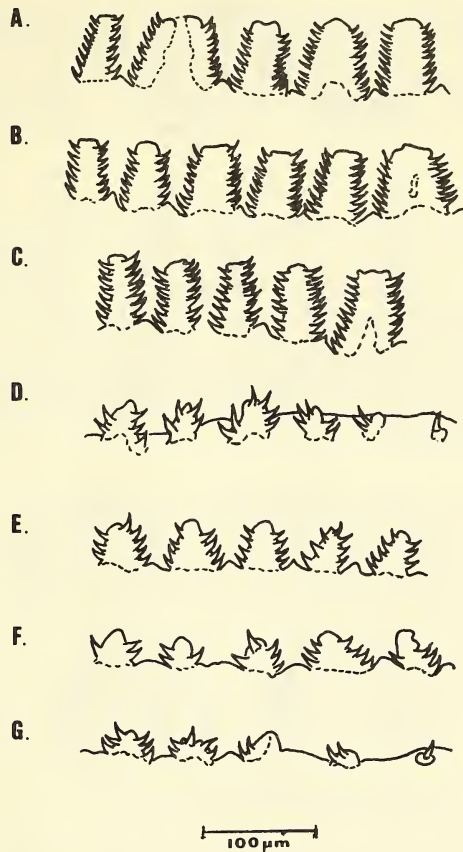   from population A

100 μm

Fig 8 Microbranchiospines from:
    A-C Anterior faces of second, third and fourth gill arches from a fish of total length 71 mm from Spring A
    D   Posterior face of fourth gill arch from the same fish
    E-G Anterior faces of second, third and fourth gill arches from a fish of total length 69 mm, from Spring E (*S. percivali*)

The distribution and size of microbranchiospines was found to differ in fish from the six populations studied. Within each population the number of denticles per microbranchiospine was seen to increase with the length of the fish (fig. 7). Microbranchiospines were absent from 13 out of 20 fish examined from population E (*S. percivali*). In those fish where they were present, they were small, with few denticles, and often did not occur in more than the central region of the gill arch, (see fig. 8).

In population A the microbranchiospines were most fully developed, and in many cases covered both faces of the fourth gill arch. The presence of microbranchiospines on the inner face of the fourth gill arch in population A, was limited to specimens over 60 mm total length and in population D to specimens over 70 mm total length. Only in one specimen were microbranchiospines found on both faces of the second and third gill arches. This fish from spring D, was 95 mm long and had no trace of microbranchiospines on the inner face of the fourth gill arch (see table 6).

The first part of the microbranchiospine to develop is a bony plate. Denticles are formed on these plates, which enlarge as more denticles are added. The width of the base of mature microbranchiopines was found to remain fairly constant at around 40 μm. Their number increases with the growth of the fish. A fish 96 mm long was found to have 122 gill filaments and 140 microbranchiospines on the outer face of the second gill arch. A fish from the same population, 70 mm long, had 112 filaments and 114 microbranchiospines in the same position. Observation showed that the increase cannot be accounted for by the growth of new microbranchiospines between existing ones. Instead what happens is that some of the existing ones divide to form two. The base of the microbranchiospine gradually widens and the

TABLE 6

Distribution of Microbranchiospines on the anterior and posterior faces of Gill arches two, three and four

Spring	Gill arch 2 ant.	post.	Gill arch 3 ant.	post.	Gill arch 4 ant.	post.
A	yes	—	yes	—	yes	some
B	yes	—	yes	—	yes	—
C	yes	—	yes	—	yes	—
D	yes	—	yes	—	yes	some
E	some	—	some	—	some	—
F	yes	some	yes	some	yes	—

bony plate eventually forms a U-shape. This shape is also seen in *C. gibbosus* (Gosse 1956). Denticles form on the inner side of the U and the tip breaks to form two new microbranchiospines. These are initially inclined towards one another and have a greater number of denticles on the outer sides than on the inside of the U, (see fig. 9).
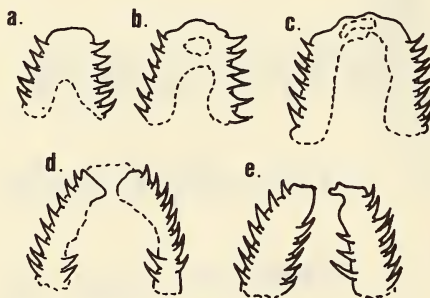

Fig 9 Progressive stages in the replication of microbranchiospines.

The function of the microbranchiospines is uncertain. Whitehead (1959) suggests that they may act in conjunction with mucus to trap small particles of food in the respiratory current. Sections taken from the gill arches and buccal cavity failed to demonstrate an increased amount of mucus secretion goblet cells in the vicinity of the microbranchiospines. Similar sections of gill arches from *S. alcalica* which was found to possess no microbranchiospines, showed a similar distribution of goblet cells. It therefore seems unlikely that this is their true function, at least in the fish examined. If balls of mucus were to be trapped, there already exists a perfectly efficient gill raker sieve, and the evolution of a totally separate set of structures seems unlikely. Furthermore, microbranchiospines were found to be totally absent from the first gill arch, and only present on both sides of the remaining gill arches on a very few fish. The gill raker sieve of *S. esculenta* was considered sufficient to prevent the loss of balls of mucus and food particles (Greenwood 1953) and such a mechanism may explain the presence of diatoms and other fine particles in the intestines of all fish examined.

COLOURATION

Vision is probably the dominant sensory modality in Cichlid fishes, and their colouration can be used as a systematic guide. In the *Sarotherodon* studied the female appears to select the male which, in common with other Cichlids, dons a striking breeding livery.

Breeding Colouration.

Springs A, B and C:– Flanks: dark greenish brown with red wash near head, margins of scales yellow, more so along mid-line. Head: dark brown with purple wash near snout. Opercula: brown with red wash, the opercular spot inconspicuous. Margins of eyes: silvery. Lower lip: white. Upper lip: grey or purple. Throat and belly: varies from dusty-blue to a dark blue-black during courtship or aggressive behaviour. Dorsal: dark brown with red lappets, becoming lighter towards the base of the spines. Soft rays: golden brown with blue-green spots and a darker margin. Anal: as dorsal but with no red lappets. Pectorals: clear with red rays. Pelvics: grey becoming darker during courtship. Caudal: golden brown with red margin and blue-green spots on membranes.

Spring D fish differ in having more yellow in the flanks giving a generally lighter colour:– Belly: greenish-blue becoming blue-black during courtship. Dorsal: with reddish spots on yellow brown rays. Caudal: with a more general reddish colouration than above.

Spring E. *S. percivali* differ from the former in being more uniform golden in colour, there being no marked variation to the scale margins:– Anal: yellow with grey spines. Throat and belly: white varying to a light blue during courtship. The caudal and pectoral fins contain more orange than the other populations.

DISCUSSION

Spring E, *S. percivali*, was the most isolated of the springs studied. Geological evidence suggests that this has always been the case (Williams 1966, Jennings 1967). The fish from this spring were differentiated from others studied by the presence of 14 dorsal spines in 42% of the population. Further differences were the shape of the premaxillae, the greater tendency towards the more specialised tricuspid teeth and the smaller length–depth ratio of the caudal peduncle. The microbranchiospines in *S. percivali* were either absent or greatly reduced in comparison to the other populations examined. *S. percivali* also shows a noticeably different male breeding livery although it clearly belongs to the *S. spilurus* type. Without detailed observations on the *Sarotherodon* from the Uaso Ngiro no firm conclusion can be drawn as to the affinities of the fish from the other springs. Each of these populations exhibit minor differences, the most important of which is the presence of approximately 20% fish with four anal spines in Springs C and F.

Comparison of the present day *S. percivali* with the syntypes show that the meristic characters and morphology of the fish in any one spring may change within a fairly short time. For this to occur a high degree of isolation is thought necessary. The effectiveness of the distance between springs acting as a genetic barrier was shown by the A, B and C complex springs. Only 400 metres separated A and C and the latter was found to have 20% of four-spined individuals. The almost complete removal of adult fish by predators will have an effect on the gene pool of succeeding generations so that over a period of time the characters of the fish populations are liable to vary in a more or less random fashion.

The habit of snail eating observed in Spring A, is of interest. This habit is recorded from various specialised Cichlids from lakes Malawi and Tanganyika, but is not recorded among adult *Sarotherodon*. These fish are typically feeders on phytoplankton or epiphytic or epilithic algal film, often mixed with detritus. However, the young of the same fish are often more carnivorous (Trewavas *et al* 1972, Green *et al* 1976). Those snail-eating fish from Spring A are not much larger than the young of related species found to be more carnivorous. No evidence of any specialisations for a diet including snails were found. Full digestion does not occur if the snail is not removed from the shell and it is possible that this habit is learned by one fish from another. It appears from gut analysis that once the habit is learned, snails figure as a prominent item of food in the diet.

The adoption of adult characteristics by fish of small size is common in *Sarotherodon* species and is associated with breeding at sizes smaller than normal. The size at which *Sarotherodon* mature is seen to depend on two factors, the size of the environment and the relative position of dominance of the fish concerned. This dwarfism or precocious breeding is important when one considers the effect of intense predation in the limited environments of the springs. As seen at Buffalo Springs, predators may be capable of removing all adult fish. Fry are able to survive as they are either too small or hide in vegetation. The ability of these fish to mature at a small size may explain why they are the only ones able to survive in the smaller springs.

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